

A NEW SPECIES OF THE AMMONITE GENUS *PHYSODOCERAS* HYATT (ASPIDOCERATIDAE) FROM THE HYBONOTUM ZONE (LOWER TITHONIAN) OF SOUTHERN GERMANY, WITH COMMENTS ON THE PHYLOGENY OF THE GENUS

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Abstract: We here introduce a new species of the aspidoceratid genus *Physodoceras*, *P. widerai* n. sp., the corresponding microconchs of which are represented by *Sutneria eugyra* Barthel. The *Physodoceras* succession of the upper Kimmeridgian (Pseudomutabilis to Beckeri zones) to Lower Tithonian (Hybonotum to Ciliata zones) is summarized.

Lectotypes are designated for *Perisphinctes casimirianus* Fontannes, *Aspidoceras episoides* Fontannes, *Ammonites hoplisus* Oppel, and *Ammonites aporus* Oppel.

Keywords: Jurassic • Tithonian • Submediterranean Province • Stratigraphy • Sexual Dimorphism.

Zusammenfassung: In dieser Arbeit führen wir eine neue Art der Aspidoceraten-Gattung *Physodoceras*, *P. widerai* n. sp., ein, deren zugehöriger Mikroconch durch *Sutneria eugyra* Barthel repräsentiert wird. Die *Physodoceras*-Abfolge vom Ober-Kimmeridgium (Pseudomutabilis- bis Beckeri-Zone) in das Tithonium (Hybonotum- bis Ciliata-Zone) wird zusammengefasst dargestellt.

Lectotypen werden für *Perisphinctes casimirianus* Fontannes, *Aspidoceras episoides* Fontannes, *Ammonites hoplisus* Oppel und *Ammonites aporus* Oppel designiert.

Schlüsselwörter: Jura • Tithonium • Submediterrane Provinz • Stratigraphie • Sexualdimorphismus.

Resumen. Una nueva especie del género de amonites *Physodoceras* Hyatt (*Aspidoceratidae*) de la Zona Hybonotum (Tithoniano Inferior) de Alemania del Sur, con comentarios sobre la filogenia del género. Se introduce una nueva especie del género *Physodoceras* (Familia Aspidoceratidae), *Physodoceras widerai* n. sp., la microconcha correspondiente esta representada por *Sutneria eugyra* Barthel. Se analiza la sucesión que representa el linaje *Physodoceras* en el Kimmeridgiano superior (Zonas Pseudomutabilis a Beckeri) y Tithoniano Inferior (Zonas Hybonotum a Ciliata).

Se designan lectotipos para *Perisphinctes casimirianus* Fontannes, *Aspidoceras episoides* Fontannes, *Ammonites hoplisus* Oppel, y *Ammonites aporus* Oppel.

Palabras clave: Jurásico • Tithoniano • Provincia Submediterránea • Estratigrafía • Dimorfismo sexual.

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INTRODUCTION

After more than twenty-five years of our study of the ammonite faunas and stratigraphy of the Upper Jurassic in southern Germany, a significant collection of well-preserved specimens accumulated. One of the most relevant outcrops for sampling Tithonian ammonites not only in southern Germany but in the entire Submediterranean Province is a large limestone quarry east of the village Liptingen, several kilometres south of the Danube Valley (Fig. 1). Some parts of the ammonite fauna from this quarry were previously described and discussed by Zeiss (1994), Schweigert & Scherzinger (1995), Schweigert (1996), Zeiss et al. (1996), Dimke (1997, unpublished thesis), Dimke & Zeiss (1997), Scherzinger et al. (2006, 2015), and Scherzinger & Schweigert (2016). The material is excellently preserved and fairly common in the beds adjacent to a large siliceous-sponge/microbial buildup, which is the main target of exploiting pure limestones for high-quality industrial products. Within the section several remarkably large olistholiths occur within the bedded limestones which were derived from the nearby autochthonous reef.

A group of aspidoceratid ammonites collected in this quarry as well as in several additional localities of the same area (Fig. 1) and in the abandoned Laisacker Quarry near Neuburg an der Donau in southern Franconia show significant characteristics, pointing to a still undescribed species. The differences in comparison with preexisting taxa have been commonly overlooked by previous authors (e.g. Schairer & Barthel 1979), who lumped them in “*Aspidoceras*” *longispinum* (Sowerby) and “*Aspidoceras*” *episoides* (Fontannes). We here demonstrate that the macroconchs of these ammonites can be differentiated from both *Physodoceras longispinum* and *Physodoceras episoides* by their sculptural features, which are mainly noted from complete, well-preserved specimens. Biostratigraphically, the new material comes from the *laisackerensis* H_{z.} of the Lower Tithonian Hybonotum Zone, whereas *Physodoceras longispinum* occurs in younger parts of the Pseudomutabilis Zone, and *Physodoceras episoides* in the Beckeri Zone, Ulmense Subzone, of the Upper Kimmeridgian.

The main purpose of this report is to describe this new species of *Physodoceras* from the *laisackerensis* H_{z.}. Finally, we comment on the species of the genus *Physodoceras* and the corresponding microconch *Sutneria*, which, in the context of the revised succession of ammonite horizons, show a well-delimited lineage through the late Kimmeridgian and early Tithonian.

SYSTEMATIC PALAEONTOLOGY

The material described is housed in the Staatliches Museum für Naturkunde Stuttgart, Germany (SMNS), the Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany (BSPM), and in the private collection of one of the authors (AS). Abbreviations: macroconch (female): [M], microconch (male): [m]. Measurements are indicated as follows: diameter (*D*), diameter at the last adult septum (*D_{ls}*), adult diameter at peristome (*D_p*), umbilical width (*U*), whorl width (*W*),

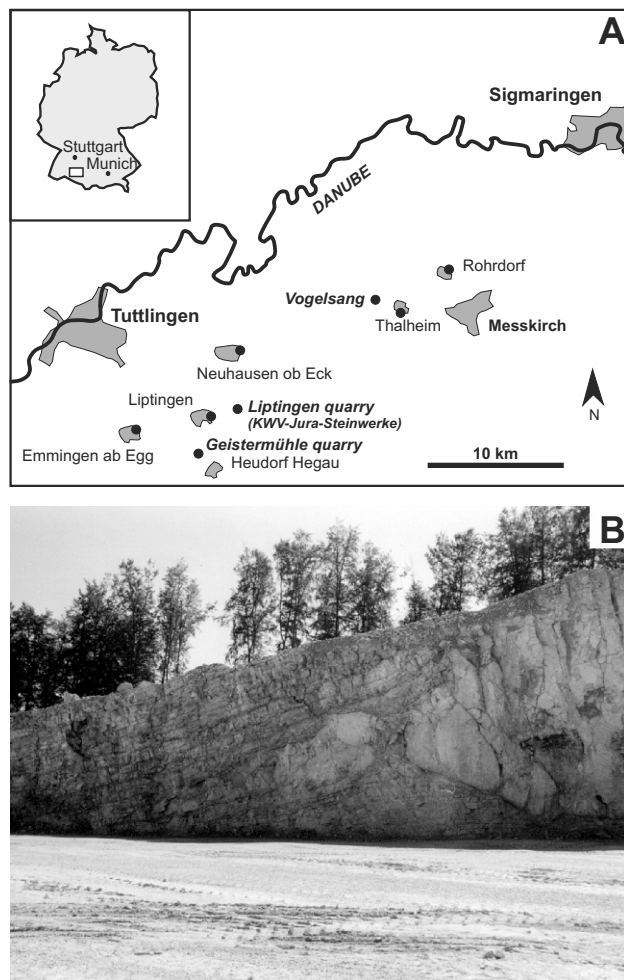


Figure 1. A: The most important Tithonian localities mentioned in the text. Gray areas indicate urbanized areas; black points indicating location of sections or quarries. B: Former wall of Liptingen Quarry (exposed to NE direction, date of photograph 2004, A.S.). The wall shows the higher part of the limestone beds of the *laisackerensis* H_{z.}. From this part of the quarry most of the specimens of *Physodoceras widerai* n. sp. come from.

whorl height (*H_l*), and whorl ventral (or apertural) height (*H_v*), all given in millimetres [mm]; length of bodychamber (*L_{bc}*) in degrees [°].

Superfamily Perisphinctoidea Steinmann, 1890
Family Aspidoceratidae Zittel, 1895
Subfamily Aspidoceratinae Zittel, 1895
Genus *Physodoceras* Hyatt, 1900

Type species. *Ammonites circumspinosus* Oppel, 1863, by original designation (= subjective junior synonym of *Ammonites inflatus circumspinosus* Quenstedt, 1857).

Remarks. The genus has been characterized by Schindewolf (1925), Wegele (1929), Arkell et al. (1957); Checa (1985) and Fözy & Scherzinger (2013a, b) provided more detailed characterizations of the genus. Nevertheless, the adult macroconch bodychamber was rarely included in

these descriptions. *Physodoceras* Hyatt [M] and *Sutneria* Zittel [m] present a dimorphic couple (see Enay 1977, Schweigert 1997, and Parent et al. 2008), with a distribution in the western Tethyan Realm, peri-Tethyan basins and shelves, and in the Subboreal, Andean and Indo-Madagascan provinces (e.g. Oppel 1863, Steuer 1897, Ilovaisky & Florensky 1941, Collignon 1960, Geyer 1969, Callomon & Cope 1971, Zeiss 1979, Scherzinger & Mitta 2006, Parent et al. 2011).

Schweigert (1998) has demonstrated that *Sutneria* belongs to the family Aspidoceratidae by the possession of a laevaptychus and Parent et al. (2008) presented for first time evidence of an intra-sexual “polymorphism” in the aspidoceratid *Physodoceras hermanni* (Berckhemer) [M]/*Sutneria subeumela* Schneid [m] from the Upper Jurassic (Beckeri Zone, Subeumela Subzone, *subsidents* horizon) of Swabia, SW Germany. There were recognized two size-classes in the macroconchs, leading to small and large adults and the case of possible sexual change in subadult stage (possible hermaphroditism). Recently, Chandler (2018) introduced the term “mesoconch” for the small-sized females, which is also applicable to our material.

The genus *Physodoceras* originally comprised moderately involute aspidoceratids with a dense periumbilical row of spines. This purely morphological classification, as applied in the last comprehensive revision by Checa (1985), is expanded here in our concept of the genus. Considering not only the type species *P. circumspinosum* (Quenstedt) but also its microconchiate partner *Sutneria platynota* (Reinecke) as well as their phyletic predecessors and successors, it becomes evident that some forms of this long-ranging lineage bear a second row of spines at least in some ontogenetic stages, and others are even lacking both rows of spines, sometimes even within a coeval population.

Physodoceras widerai n. sp.

Figs. 2-5

- 1979 *Aspidoceras episoides* Fontannes. – Schairer & Barthel: 14, pl. 3: 1.
 1979 *Aspidoceras longispinum* (Sowerby). – Schairer & Barthel: 18, fig. 3a-c, e, g-k, pl. 3: 4-8, pl. 4: 1, 3-6.
 1995 bispinose Aspidoceraten. – Schweigert & Scherzinger: 314.
 1995 *Schaireria episoides* (Fontannes). – Schweigert & Scherzinger: 314.
 1996 *Schaireria episoides* (Fontannes) [M]. – Schweigert: 298.
 1996 *Aspidoceras* sp. (bispinose Form) [M] – Schweigert: 299.
 1996 *Aspidoceras* sp. – Zeiss et al.: 134.
 1996 *Physodoceras episoides* (Fontannes). – Zeiss et al.: 134.
 1997 *Aspidoceras* sp., cf. *hoplisum* (Oppel). – Dimke: 37.
 1997 *Aspidoceras* sp. (bispinose Form). – Dimke: 37, tab. 3.
 1997 *Schaireria episoides* (Fontannes). – Dimke: 37, tab. 3.
 1997 *Aspidoceras* sp., cf. *catalaunicum* (de Loriol). – Dimke & Zeiss: 77, tab. 1, pl. 12, fig. 1.
 1997 *Aspidoceras* sp., cf. *hoplisum* (Oppel). – Dimke &

Zeiss: 77, tab. 1, pl. 9, fig. 1.

- 1997 *Aspidoceras* sp. (bispinose Form). – Dimke & Zeiss: 79, tab. 1.
 1997 *Schaireria episoides* (Fontannes). – Dimke & Zeiss: 79, tab. 1.
 2013 *Aspidoceras episoides*, *Aspidoceras longispinum*. – Fözy & Scherzinger: 185.
 2013 “*Aspidoceras longispinum*”. – Fözy & Scherzinger: 245.
 2016 *Physodoceras* sp. – Scherzinger & Schweigert: 290, fig. 3.

Type locality and section. Liptingen Quarry, Baden-Württemberg, SW Germany (Fig. 1).

Type horizon. Hangende-Bankkalke Formation, *laisackerensis* Hz., Hybonotum Z., Lower Tithonian.

Type specimens (macroconchs). Holotype (SMNS 70414/1), Paratype I (SMNS 70414/2), Paratype II (SMNS 70414/3), Paratype III (SMNS 70414/4), Paratype IV (SMNS 70414/10), Paratype V (SMNS 70414/11), Paratype VI (SMNS 70414/12), Paratype VII (SMNS 70414/13), Paratype VIII (SMNS 70414/14), Paratype IX (SMNS 70414/10), Paratype X (SMNS 70414/11), and Paratype XI (SMNS 70414/12).

Additional material. *Macroconchs*: SMNS 70414/13 – 70414/16 (unfigured), BSPM 1957 II 409 [Laisacker], BSPM 1957 II 412 [Laisacker], BSPM 1957 II 413 [Laisacker], BSPM 1957 II 411 [Laisacker], BSPM 1957 II 430 [Laisacker], BSPM 1957 II 427 [Laisacker]. *Microconchs* (termed as *Sutneria eugyra*): SMNS 70414/5 to 70414/9 [Liptingen], SMNS 62620 [Rohrdorf], BSPM 1957 II 2, Holotype in Barthel (1959) [Laisacker], BSPM 1957 II 3 to 6 Paratypes in Barthel (1959) [Laisacker], BSPM 1957 II 139 Paratype in Barthel (1959) [Laisacker], BSPM 1957 II 140 [Laisacker].

Etymology. After our friend Damian Widera, who allowed and supported the field works and sampling in the Liptingen Quarry.

Diagnosis. Macroconchs small to large-sized, adult diameter from 30 to 300 mm, but mostly small-sized. More or less compressed-suboval in whorl section with one row of lateral tubercles up to 20-30 mm diameter, then more depressed, bituberculated, with an additional periumbilical row of tubercles. Small specimens with fine striae, larger ones with upper part of flank and venter coarsely striated. Microconchs 15-30 mm in diameter at adult peristome, rather compressed, involute; adult bodychamber smooth or with falcoid striae, with moderately long and straight lappets.

Description. The holotype is an almost complete adult macroconch with maximum $D = 258$ mm, and last septum at about $D = 180$ mm. The adult phragmocone is evolute, with depressed whorl section, venter broadly rounded and umbilical wall high.

The large type series shows the macroconch (female) adult size is very variable, ranging from 30 to 300 mm in diameter. Based on these specimens the macroconch

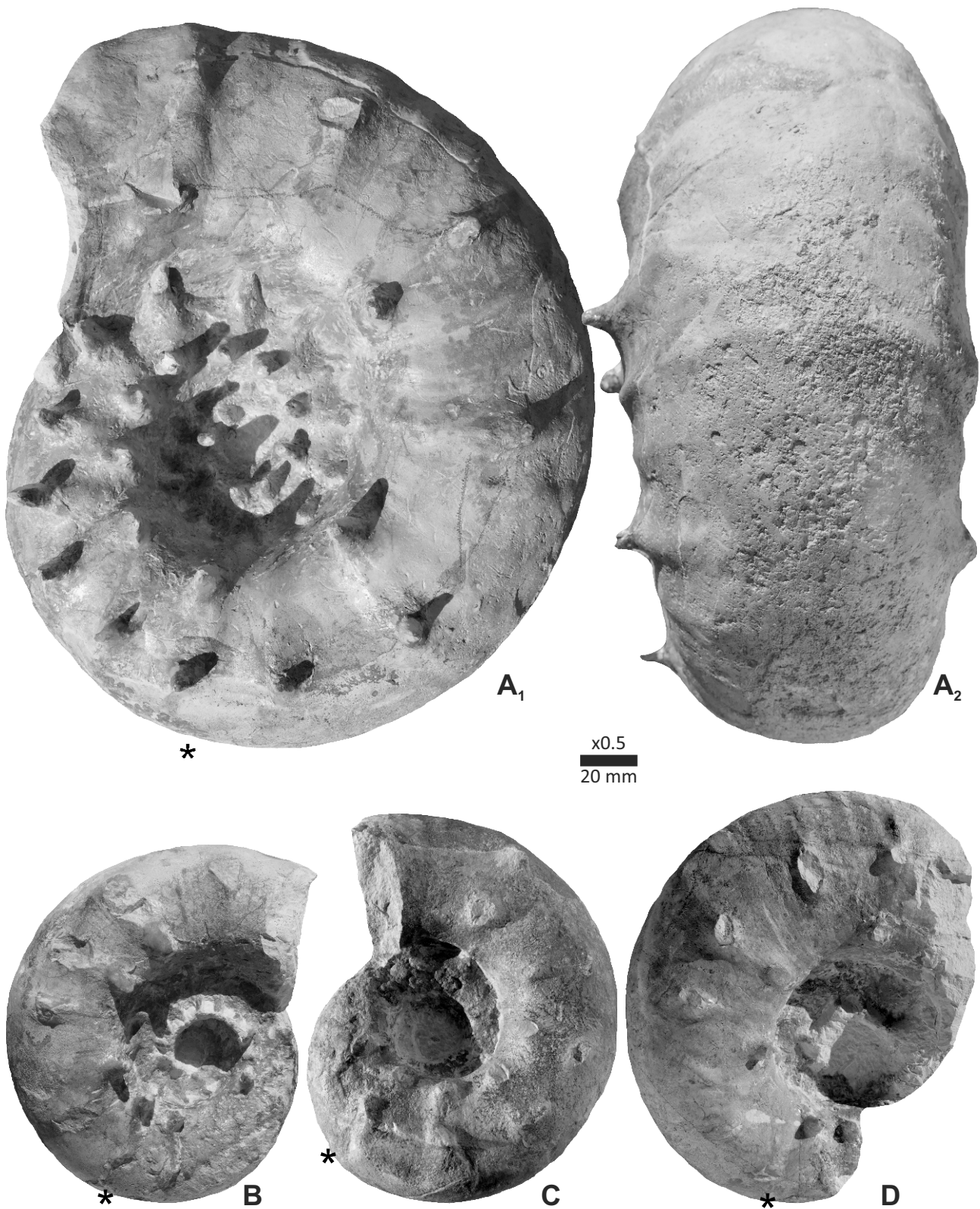


Figure 2. *Physodoceras widerai* n. sp., Liptingen Quarry, *laisackerensis* Hz., Rueppellianus Subzone, Hybonotum Zone. **A:** Holotype, lateral (A₁) and ventral (A₂) views, adult macroconch with nearly complete bodychamber showing the coarse tubercles (SMNS 70414/1); **B:** adult macroconch with incomplete bodychamber (SMNS 70414/2), Paratype I. **C:** adult macroconch with nearly complete bodychamber (SMNS 70414/3), Paratype II. **D:** adult, incomplete macroconch (SMNS 70414/4), Paratype III. – All in half size. Asterisk indicates the last septum.

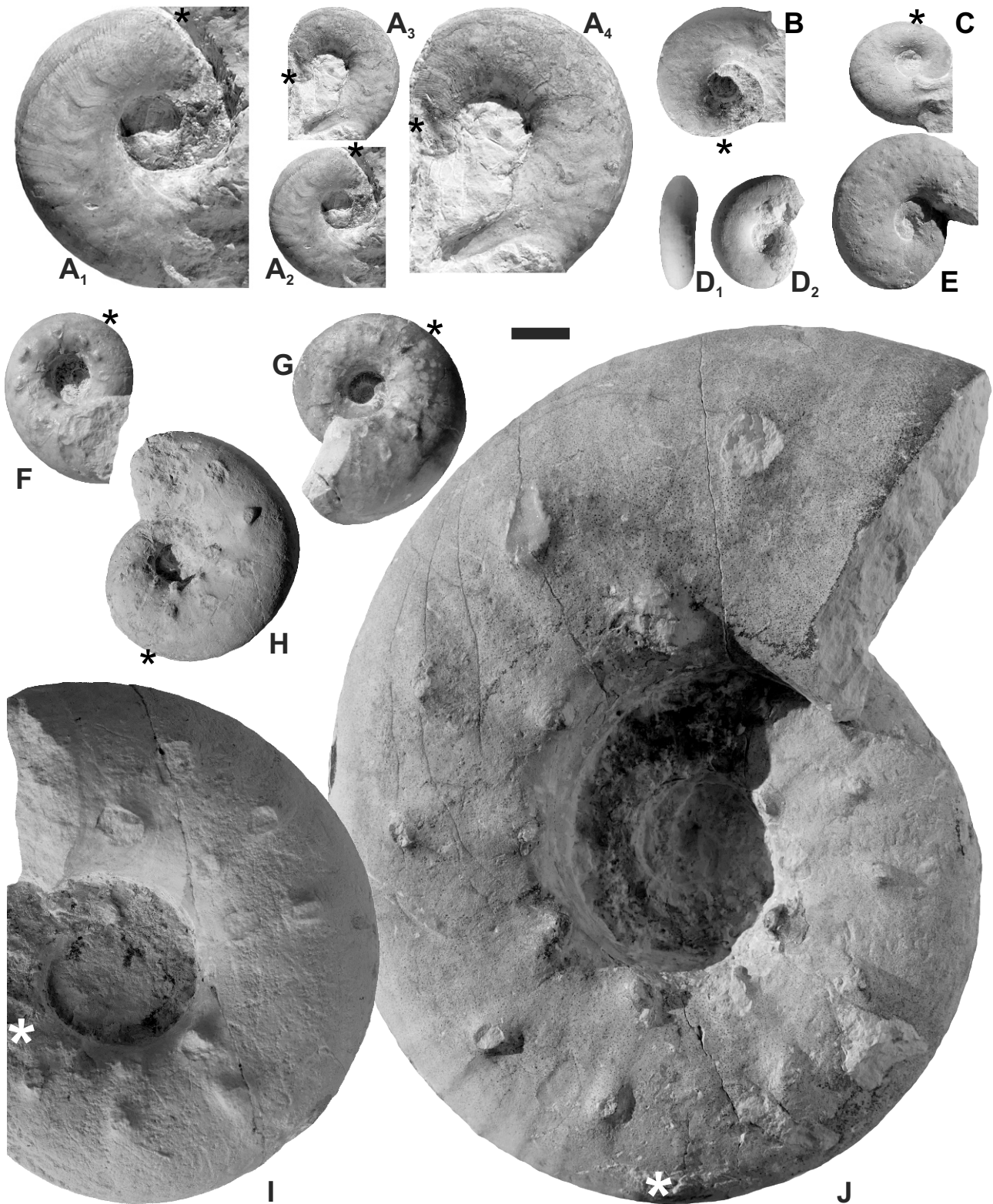


Figure 3. *Physodoceras widerai* n. sp. [M&m], Liptingen Quarry, *laisackerensis* Hz., Rueppellianus Subzone, Hybonotum Zone. **A-E:** microconchs, *Sutneria eugyra* Barthel. **A:** complete adult with bodychamber and peristome, showing the fine striae sculpture (SMNS 70414/5). **A₁-A₂:** left side (apertural view); **A₃-A₄:** right side. **B:** nearly complete specimen with bodychamber and beginning of the peristome (SMNS 70414/6). **C:** complete adult with bodychamber and peristome (SMNS 70414/7). **D:** adult with incomplete peristome, beginning of bodychamber not discernible (SMNS 70414/8). **E:** nearly complete, slightly crushed adult with bodychamber and part of peristome (SMNS 70414/9). **F-J:** juvenile macroconchs. **F:** incomplete, with a single row of tubercles at first, later followed by a second row (SMNS 70414/10), Paratype IV. **G:** same features as previous specimen (SMNS 70414/11), Paratype V. **H:** slightly crushed (SMNS 70414/12), Paratype VI. **I:** medium-sized incomplete with crushed inner whorls, showing two rows of tubercles on the outer whorl (SMNS 70414/13), Paratype VII. **J:** subadult with crushed inner whorls, showing two rows of tubercles on the outer whorl (SMNS 70414/14), Paratype VIII. – All natural size, except A₁ and A₄ double size. The asterisk indicates the last septum.



Figure 4. *Physodoceras widerai* n. sp. [M], Liptingen Quarry, *laisackerensis* Hz., Rueppellianus Subzone, Hybonotum Zone. **A:** adult, incomplete macroconch, innermost whorls crushed showing the coarse tubercles (SMNS 70414/15), note the laevaptychus preserved in the bodychamber, Paratype IX. **B:** small-sized macroconch (mesoconch) with fine striae and one row of fine tubercles (SMNS 70414/16), Paratype X. **C:** small-sized macroconch (mesoconch) with fine striae, lacking tubercles (SMNS 70414/17), Paratype XI. – All natural size. The asterisk indicates the last septum.

ontogeny of the new species can be subdivided into three stages. The later stages are shown by the larger specimens which, on the other hand are less abundant.

Stage I: from the innermost whorls, up to $D = 20\text{--}30$ mm the shell is rather involute, suboval in whorl section, with a single row of spiny tubercles on the middle of the flank (Fig. 3F-H).

Stage II: from about $D = 20\text{--}30$ mm there is a second row of tubercles, developed periumbilically (Figs. 2B, 3I, 4B).

Stage III: from about $D = 70\text{--}90$ mm the shell is more evolute, with more depressed whorl section; strong ribs developed joining the lateral and periumbilical tubercles in pairs (Figs. 2B-D, 3J). In the adult bodychamber of the largest specimens some ribs unrelated with the tubercles may appear (Figs. 2A, 4A).

Few exceptional specimens remain almost smooth, bearing only striae on the flanks (Fig. 4C).

The ontogeny of the microconch (morphospecies *S. eugyra*) differs from that of the macroconch from $D = 10\text{--}15$ mm onwards, at the beginning of the adult bodychamber in most specimens. It becomes more compressed and evolute (Fig. 3A-E), with falcate striae, in some specimens reinforced on mid-flank (Fig. 3A). The peristome develops long and straight lappets (Fig. 3A, C).

Remarks and comparison. The species is very variable, mainly the macroconchs in adult size and density and strength of tubercles of the phragmocone. The striae are not always preserved.

The microconchs of *P. widerai* n. sp. correspond to the early representatives of the morphospecies *Sutneria eugyra* Barthel, 1959.

From the next older horizon (*riedlingensis* Hz., Rueppellianus Subzone, Fig. 5) a similar macroconch is known, but apparently differing by the earlier onset of strong bituberculation (Fig. 6E). However, that material is not yet enough for closer comparisons.

From the next younger horizons (*rueppellianus-moernsheimensis* horizons, Fig. 5) the macroconchs of *Physodoceras pipini* (Oppel) are more involute and compressed, with higher flanks, and have only periumbilical tubercles through the adult phragmocone and bodychamber (Fig. 6F herein; see also Schlegelmilch 1994: pl. 72: 2, neotype). The microconchs correspond to the later representatives of *S. eugyra* (Fig. 6G) which are practically indistinguishable from the earlier representatives.

As noted in the introduction chapter and detailed in the synonymy, Schairer & Barthel (1979) figured as *Aspidoceras longispinum* and *Aspidoceras episoides* several specimens, which belong to *P. widerai* n. sp. [M]. This reassignment is based on differences of stratigraphic age and morphology of the type specimens, as well as the distinct sexual dimorphism of these species.

Physodoceras longispinum is very similar to *P. widerai* n. sp., in such a way that their macroconchs are hardly distinguishable if not some differences in the inner whorls can be observed from at least moderately well preserved material. The inner whorls of the holotype of *P. longispinum* have more densely spaced umbilical tubercles from which

born mild ribs, which extend up to the lateral tubercles (see Callomon & Cope 1971: pl. 12: 1-2). The umbilical tubercles and the ribs appear later in *P. widerai* n. sp. [M], in the subadult-adult ontogeny (see Figs. 2, 3I-J, 4). However, both species can be clearly differentiated by their sexual dimorphism, where the microconch of *P. longispinum* (*S. eumela*) is strongly ribbed in the adult bodychamber, but almost smooth in the microconch of *P. widerai* n. sp. (*S. eugyra*, see Fig. 3A-E). However, the much deeper stratigraphic position of *P. longispinum* in the upper Pseudomutabilis Zone should allow to prevent confusions by this close homoeomorphy of the macroconchs.

According to Fontannes (1879: 101) the type series of *Aspidoceras episoides* (relatively small macroconchs) show the inner whorls smooth or finely striated with depressed, wider than high whorl section. The outer whorls ($D = 50\text{--}76$ mm according to his measurements) are evolute, rounded in whorl section, smooth or with mild tubercles or wide and rounded plications on the umbilical shoulder. The macroconchs of *P. widerai* n. sp. are tuberculated from the inner whorls as described above. The rare smooth variants of *P. widerai* n. sp. (Fig. 4C) are very similar but more involute. The microconch of *P. episoides* (*S. bracheri*) is stouter and periumbilically tuberculated with finely ribbed venter in comparison with the microconch of *P. widerai* n. sp. (*S. eugyra*), which is usually slender with the umbilical area smooth or finely striated.

Occurrences and distribution. The described material comes from the Liptingen Quarry, Baden-Württemberg, SW Germany (Fig. 1); these occurrences represent the *laisackerensis* Hz., Rueppellianus Subz., Hybonotum Z., Lower Tithonian (Fig. 5). Additional material from the same ammonite faunal horizon, not illustrated herein, but anyway part of our studied material, comes from Neuhausen ob Eck, Emmingen ab Egg, Heudorf im Hegau (abandoned Geistermühle Quarry), Rohrdorf, Vogelsang and Thalheim near Meßkirch (all Swabia), and from Laisacker near Neuburg an der Donau (Franconia, Bavaria).

THE SUCCESSION OF SPECIES OF *PHYSODOCERAS* AND *SUTNERIA* IN SOUTHERN GERMANY

A brief account of the stratigraphic distribution of the genus *Physodoceras* (including the corresponding microconch genus *Sutneria*) was given by Fözy & Scherzinger (2013a, b). The new material and additional stratigraphical information allow us to offer an expanded revision of the successive species through the Pseudomutabilis, Beckeri, Hybonotum, Mucronatum, Vimineus and Ciliata zones. The following discussion is based on the studied material, new records, type specimens in different collections and most relevant papers dealing with species of the genera (e.g. Geyer 1969, Zeiss 1979, Checa 1985, and references therein).

The revised succession of species of *Physodoceras* given in detail below, mainly based on the records from Southern Germany, is depicted in Fig. 5. It has an obvious phylogenetic meaning: evolutionary steps inferred from more or less notorious morphologic changes and sexual dimorphism. We must assume that this record is mainly the

Stage	Zone	Subzone	Biohorizon		
TITHONIAN	Ciliata		<i>ciliata</i>	<i>P. neoburgense</i>	<i>S. asema</i>
			<i>penicillatum</i>		
	Vimineus		<i>vimineus</i>		
	Mucronatum		<i>levicostatum</i>	<i>P. cf. pipini</i>	<i>Sutneria</i> sp.
			<i>franconicum</i>		
	Hybonotum	Moe.	<i>moernsheimensis</i>	<i>P. pipini</i>	<i>S. eugyra</i>
		Rueppellianus	<i>rueppellianus</i>		
			<i>laisackerensis</i>	<i>P. widerai</i> n. sp.	
			<i>riedlingensis</i>		
		Riedense	<i>eigeltینگense</i> β	<i>P. hoplisus</i>	<i>S. apora</i>
			<i>eigeltینگense</i> α		
		Ulmense	<i>rebouletianum</i>	<i>P. episoides</i>	<i>S. bracheri</i>
			<i>hoelderi</i>	<i>P. nattheimense</i>	<i>S. cf. rebholzi</i>
			<i>zio-wepferi</i> β	<i>P. episum</i>	<i>S. rebholzi</i>
			<i>zio-wepferi</i> α		
KIMMERIDGIAN	Beckeri	Setatum	<i>siliceus</i>		
			<i>uracensis</i>		
			<i>ornatum</i>	<i>P. eligmoptychum</i>	<i>S. casimiriana</i>
			<i>supinum</i>		
			<i>minutum</i>		
		Subeumela	<i>fischeri</i>		
			<i>subsidens</i>	<i>P. hermanni</i>	<i>S. subeumela</i>
			<i>kiderleni</i>		
			<i>pedinopleura</i>	<i>Physodoceras</i> sp.	<i>S. pedinopleura</i>
	Pseudomutabilis	Pseudomutabilis	<i>semicostatum</i> γ	<i>P. longispinum</i>	<i>S. eumela</i> morph lorioli
			<i>semicostatum</i> β		
			<i>semicostatum</i> α	<i>P. cf. longispinum</i>	<i>S. eumela</i> morphs eumela (rare), lorioli
			<i>pseudom.-eudoxus</i> β	<i>P. sesquinodosum</i>	<i>S. eumela</i> morphs eumela, lorioli
			<i>pseudom.-eudoxus</i> α		
		Schilleri	<i>eumela-levipictus</i>	<i>P. cf. sesquinodosum</i>	<i>S. eumela</i> morph eumela
			<i>prominens-hoelderi</i> β	<i>P. cf. haynaldi</i>	<i>S. hoelderi</i>
			<i>prominens-hoelderi</i> α	<i>P. cf. acanthicum</i>	
	Acanthicum Zone			<i>P. acanthicum</i>	<i>Sutneria</i> sp.

Figure 5. Chronostratigraphy and ammonite horizons of the Pseudomutabilis to Ciliata zones in the Upper Jurassic of Southern Germany, with indication of the stratigraphic ranges of the species of *Physodoceras* (corresponding microconchs termed as *Sutneria*). Succession of biohorizons according to Schweigert (2015), Scherzinger et al. (2015, 2016), Scherzinger & Schweigert (1999, 2003, 2004, 2016). The gaps in the fossil record in the intervals of the *minutum-supinum* and *uracensis-siliceus* horizons are probably caused by unfavorable palaeoecological conditions. Abbreviations: *pseudom.-eudoxus* α, β for *pseudomutabilis-eudoxus* α, β horizons; Moe. for Moernsheimensis Subzone.

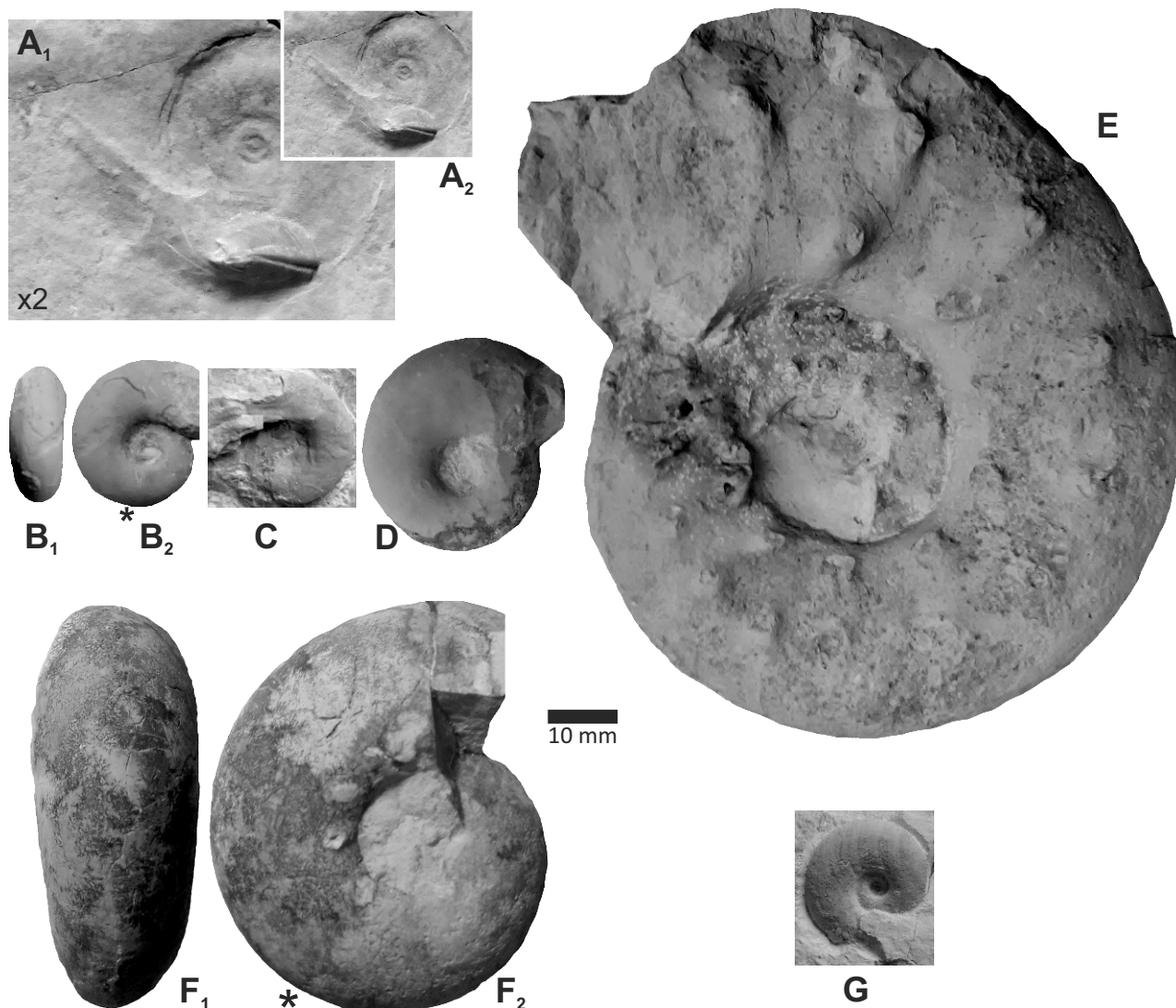


Figure 6. Additional ammonites of the genus *Physodoceras* and morphogenus *Sutneria*. **A:** *Sutneria apora* (Oppel), adult microconch (SMNS 70461, leg. Martin Röper) showing the laevaptychus still in situ, like in the type specimens of Oppel (1863); Painten Formation of Painten, Franconia, Early Tithonian, *eigeltingense* β Horizon. **B-D:** *Sutneria apora* (Oppel), adult microconchs (SMNS 70462/1-3) from a section close to railway, 1 km NW of Talmühle Hamlet, N of Engen, SW Germany; Hangende-Bankkalke Formation, Lower Tithonian, Hybonotum Zone, Riedense Subzone, *eigeltingense* α horizon. **E:** *Physodoceras* cf. *widerai* n. sp., adult macroconchiate phragmocone (SMNS 70463), Liptingen Quarry (lower part of the section, level 11a in Scherzinger & Schweigert 2016: fig. 3), between the *riedlingensis* and *laisackerensis* horizons. **F:** *Physodoceras pipini* (Oppel), adult macroconch (SMNS 70460/1), Hybonotum Zone, *moernsheimensis* Hz. of Mörsheim. **G:** *Sutneria eugyra* Barthel, adult microconch with lappets (SMNS 70460/2), *moernsheimensis* Horizon of Mörsheim. – Natural size (x1), except A₁ (x2) and E (x0.5). Scale bar: 10 mm except for A₁ (5 mm) and E (20 mm).

result of local adaptations but also influenced by regional migratory effects. For example, the Mediterranean ammonite *Mesosimoceras cavouri* (Gemmellaro, 1872) is recorded from the upper Pseudomutabilis Zone of SW Germany (Scherzinger et al. 2016), suggesting a time of favourable conditions for faunal exchange from the western Tethys. In this sense the succession in Fig. 5 can be interpreted as the regional development of the *Physodoceras* lineage in the interval from the Pseudomutabilis to the Ciliata zones.

As noted above, *Physodoceras* has an almost worldwide palaeogeographic distribution, reaching even Subboreal regions. This pattern and the commonly high

intraspecific variability, which characterizes every transient along with the rare occurrence of complete adult macroconchs, have led to the proliferation of a large number of local morphospecies, many of them introduced with no or poor stratigraphic information. This situation obscures severely the local successions for comparison.

Acanthicum Zone, Kimmeridgian

Physodoceras acanthicum (Oppel, 1863) [M]. Lectotype (from Thalmässing, Bavaria, Germany) in Neumayr (1873: pl. 41).

Sutneria sp. [m].

Pseudomutabilis Zone, Kimmeridgian**hoelderi-prominens α horizon, Schilleri Subzone**

Physodoceras cf. *acanthicum* (Oppel, 1863) [M]

Sutneria hoelderi Zeiss, 1979 [m]. Holotype (from Crussol, France) in Hölder & Ziegler (1959: pl. 21: 4).

hoelderi-prominens β horizon, Schilleri Subzone

Physodoceras cf. *haynaldi* (Herbich in Neumayr, 1873) [M]. The holotype (from Ciofronca-Lacul Roşu, East Carpathians, according to Săsăran 2016: 12) of *Aspidoceras haynaldi* was illustrated by Neumayr (1873: pl. 42: 3) by a drawing, later refigured by Herbich (1878: pl. 14-15: 1a-1b).

Sutneria hoelderi Zeiss [m].

eumela-levipictus horizon, Schilleri Subzone

Physodoceras cf. *sesquinosum* (Fontannes in Dumortier & Fontannes, 1876) [M].

Sutneria eumela (d'Orbigny, 1847) [m] morph *eumela* (typical morph, see below). Lectotype (from Mauvage, Meuse, France) designated and refigured by Zeiss (1979: pl. 3: 1-3).

pseudomutabilis-eudoxus α horizon, Pseudomutabilis Subzone

Physodoceras sesquinosum (Fontannes in Dumortier & Fontannes, 1876) [M]. Fontannes (in Dumortier & Fontannes 1876: 126-128) described the species based on six specimens, and in p. 127 he mentioned the “type”, which refers to the specimen figured in his plate 18, fig. 6, and its measurements indicated in p. 126. This specimen should be therefore considered the holotype, refigured photographically by Checa (1985: pl. 3: 3).

Sutneria eumela (d'Orbigny, 1847) [m] morphs *eumela* and *lorioli*. The latter morphotype is characterized by the holotype of *Sutneria lorioli* Zeiss (1979: fig. 5, refigured from Loriol et al. 1872: pl. 3: 6) which is here considered an infrasubspecific variant of *S. eumela*.

pseudomutabilis-eudoxus β horizon, Pseudomutabilis Subzone

Physodoceras sesquinosum (Fontannes in Dumortier & Fontannes, 1876) [M]

Sutneria eumela (d'Orbigny, 1847) [m] morphs *eumela* and *lorioli*.

semicostatum α horizon, Pseudomutabilis Subzone

Physodoceras cf. *longispinum* (Sowerby, 1825) [M]

Sutneria eumela (d'Orbigny, 1847) [m] morphs *eumela* (rare) and *lorioli*.

semicostatum β -semicostatum γ horizons, Pseudomutabilis Subzone

Physodoceras longispinum (Sowerby, 1825) [M]. Holotype (probably from south of Weymouth, England) refigured in Callomon & Cope (1971: pl. 12: 1-2).

Sutneria eumela (d'Orbigny, 1847) [m] morph *lorioli*.

Beckeri Zone, Kimmeridgian**pedinopleura horizon, Subeumela Subzone**

Physodoceras sp. [M]. Seeger (1958: 38) cited “*Aspidoceras contemporaneum* Favre, 1877” associated with *Sutneria pedinopleura* Seeger, 1961 from the Buchtal section near Magolsheim. Based on the only specimen figured, “*A. contemporaneum*” (Favre 1877: pl. 8: 3) can be assigned to *Physodoceras* by possessing a single row of tubercles which are periumbilical. However, Favre (1877: 65) indicates that one or two rather weak prosocline ribs born from each tubercle and run the flank.

Sutneria pedinopleura Seeger, 1961 [m]. Holotype (from south of Tuttlingen, Swabia, Germany) in Seeger (1961: pl. 3: 4).

kiderleni, subsidens and fischeri horizons, Subeumela Subzone

Physodoceras hermanni (Berckhemer, 1922) [M]. Lectotype (from Kaltental near Grabenstetten, Germany) designated and refigured in Parent et al. (2008: 183, fig. 3A).

Sutneria subeumela (Schneid, 1915) [m]. Lectotype (from Galgenberg hill near Wellheim, Franconia, Germany) designated and refigured in Parent et al. (2008: 183, fig. 3B).

ornatum horizon, Setatum Subzone

Physodoceras eligmoptychum (Fontannes, 1879) [M]. The holotype by monotypy is the specimen figured by Fontannes (1879: pl. 13: 9).

Sutneria casimiriana (Fontannes, 1879) [m]. Zeiss (1979: 264) refers to the specimen figured by Fontannes (1879: pl. 11: 4) as holotype. Nevertheless, Fontannes (1879: 74-75) described the species based on several specimens, but without designation of a type, and to our knowledge there has been no designation of a lectotype yet. Therefore, the specimen figured in Fontannes (1879: pl. 11: 4) is here designated as the lectotype.

zio-wepferi α and β horizons, Ulmense Subzone

Physodoceras episum (Oppel, 1863) [M]. Neotype (from Fridingen an der Donau, Swabia, Germany) designated and figured by Schlegelmilch (1994: 130, pl. 72: 3).

Sutneria rebholzi Berckhemer, 1922 [m]. Neotype designated and figured by Berckhemer & Hölder (1959: pl. 12: fig. 61).

hoelderi horizon, Ulmense Subzone

Physodoceras nattheimense Schweigert, 1998 [M]. Holotype (from the coral limestones of Nattheim, Swabia, Germany) in Schweigert (1998: pl. 5: 1).

Sutneria cf. *rebholzi* Berckhemer, 1922 [m] (e.g. Schweigert 1998: pl. 5: 5-7).

rebouletianum horizon, Ulmense Subzone

Physodoceras episoides (Fontannes, 1879) [M]. Schairer & Barthel (1979: 14) considered the only specimen figured by Fontannes (1879: pl. 13: 10) as the holotype. Nevertheless, Fontannes (1879: 101-102) did not designate a type specimen. In the description of the species Fontannes refers to more than a single specimen and provides three sets of measurements which probably correspond to three specimens. We take the opportunity to designate the only specimen figured by Fontannes (1879: pl. 13: 10) as lectotype.

Sutneria bracheri (Berckhemer, 1922) [m]. Holotype (from Heiland chapel near Fridingen, Swabia, Germany) refigured photographically in Barthel (1959: pl. 6: 13-14).

Hybonotum Zone, Tithonian**eigeltینگense α and β horizons, Riedense Subzone**

Physodoceras hoplisus (Oppel, 1863) [M]. Checa (1985: 80) mentioned a “holotype”, however, Oppel had 18 syntypes and illustrated 2 of them without holotype designation. We thus take the opportunity to designate here the specimen from Eichstätt (Bavaria, Germany) illustrated by Oppel (1863: pl. 73: 5) as lectotype of *Ammonites hoplisus* Oppel, 1863.

Sutneria apora (Oppel, 1863) [m]. Oppel (1863) did not designate a holotype, and to our knowledge there was no lectotype designation yet. We take the opportunity to designate the specimen from Solnhofen (Bavaria, Germany) figured by Oppel (1863: pl. 73: 2), refigured by Ziegler (1974: fig. 2), as lectotype of *Ammonites aporus* Oppel, 1863. Additional specimens in volume and another one with the laevaptychus in situ are shown in Fig. 6A-D.

riedlingensis horizon, Rueppellianus Subzone

Physodoceras cf. *widerai* n. sp. [M]. From this biohorizon there was collected (AS) a single specimen with very thick, alternating spines in two rows (Fig. 6E), similar to *P. widerai* n. sp., but differing in that the very thick spines appear earlier in the juvenile stage. The microconch is only known by a single, fragmentary specimen of *Sutneria*.

laisackerensis horizon, Rueppellianus Subzone

Physodoceras widerai n. sp. [M]. This report.

Sutneria eugyra Barthel, 1959 [m]. Holotype (from Laisacker near Neuburg an der Donau, Franconia, Germany) in Barthel (1959: pl. 6: 1-3).

rueppellianus horizon, Rueppellianus Subzone

Physodoceras pipini (Oppel, 1863) [M]. Holotype (from Solnhofen, Bavaria, Germany) in Schlegelmilch (1994: pl. 72: 2).

Sutneria eugyra Barthel, 1959 [m].

moernsheimensis horizon, Moernsheimensis Subzone

Physodoceras pipini (Oppel, 1863) [M].

Sutneria eugyra Barthel, 1959 [m].

Mucronatum Zone**franconicum and levicostatum horizons**

Physodoceras cf. *pipini* (Oppel, 1863) [M]. *Aspidoceras pipini* figured in Zeiss (1968: pl. 27: 2).

Sutneria sp. [m].

Vimineus Zone**vimineus horizon**

Physodoceras neoburgense (Oppel, 1863) [M]. Neotype (from Unterhausen near Neuburg an der Donau, Franconia, Germany) designated and figured by Schlegelmilch (1994: pl. 72: 4).

Sutneria asema (Oppel, 1865) [m]. Holotype (from Rogoznik, Carpathian Mountains, Poland) refigured by Barthel (1962: pl. 3: 8).

Ciliata Zone**penicillatum and ciliata horizons**

Physodoceras neoburgense (Oppel, 1863) [M].

Sutneria asema (Oppel, 1865) [m].

The gaps in the record of *Physodoceras/Sutneria* in the intervals of the *minutum-supinum* and *uracensis-siliceus* horizons are probably caused by unfavorable palaeoecological conditions.

The succession of corresponding macro- and microconchs (Fig. 5) shows some of the microconchs in correspondence with more than a single macroconch. The microconchs *S. hoelderi*, *S. eumela*, and *S. eugyra* change morphologically slower than the corresponding macroconchs. In the segment of the lineage represented by the macroconchs *P. sesquinosum*-*P. longispinum* (*pseudomutabilis-eudoxus* a to *semicostatum* g horizons) the corresponding microconchs are assigned to *S. eumela*. The variability of *S. eumela* is here indicated as two morphs: *eumela* and *lorioli*, the latter one becoming predominant in the *semicostatum* b and *semicostatum* g horizons, whereas the *eumela* morph is only rarely recorded in the *semicostatum* a horizon.

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